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Phytogeographical analysis of Tasmanian alpine floras

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ABSTRACT. Lists of vascular plant species were obtained from twenty-eight, disjunct, high altitude, treeless areas in Tasmania. These lists pertained to vegetation dominated by the austral-montane element of the flora which is found both above and below the usually indistinct, and often absent, Tasmanian upper slope treeline. A polythetic, agglomerative classification of the Tasmanian and four Australian mainland alpine floras resulted in five groups: the mainland mountains, the eastern Tasmanian mountains, a group extending north–south through the centre of Tasmania, western Tasmanian quartzite mountains, and western Tasmanian mountains formed from more weatherable parent material. The Tasmanian floras form a continuum closely related to mean annual precipitation and surface geology, but not strongly related to continentality. Tasmanian endemism increases strongly from east to west, and similarity values with the mainland mountain floras and the New Zealand flora show the reverse pattern. It is suggested that the variation in and between the alpine floras of Tasmania and mainland Australia may be largely related to edaphic conditions.

Introduction

The topographically subdued continent of Australia contains few areas above the climatic treeline (Costin, 1972). However, the alpine vegetation of Australia has an importance far beyond its area. Alpine plant communities play a vital role in the regulation of water yield from some of the few high rainfall areas on the continent (Wimbush & Costin, 1979). They also have considerable biogeographic interest given the floristic affinities between the alpine vegetation of Australia, New Zealand and southern South America (Godley, 1960). While the ecology and floristic composition of the major areas of alpine vegetation on the mainland of Australia are well researched (e.g. Costin *et al.*, 1979), the Tasmanian vegetation has been assumed to fit the patterns described for Cradle Mountain (Sutton, 1928), Mt Wellington (Martin, 1940) and the Central Plateau (Jackson, 1972). Recently published descriptive work (Kirkpatrick, 1977, 1980; Kirkpatrick & Harwood, 1980) has indicated that Tasmanian alpine vegetation is highly heterogeneous, and that the generalizations that Costin (1957) was able to make in relation to the Australian mainland alpine vegetation may not be possible in Tasmania. This paper attempts to give a broad outline of the nature of heterogeneity in Tasmanian alpine vegetation through an analysis of species lists from twenty-eight disjunct areas (Fig. 1), and considers the relationships of the Tasmanian floras to those of the mainland and New Zealand and environmental factors.

Alpine, subalpine and treeline in Tasmania

McVean (1969) has suggested that the Tasmanian mountains are less 'alpine' than those

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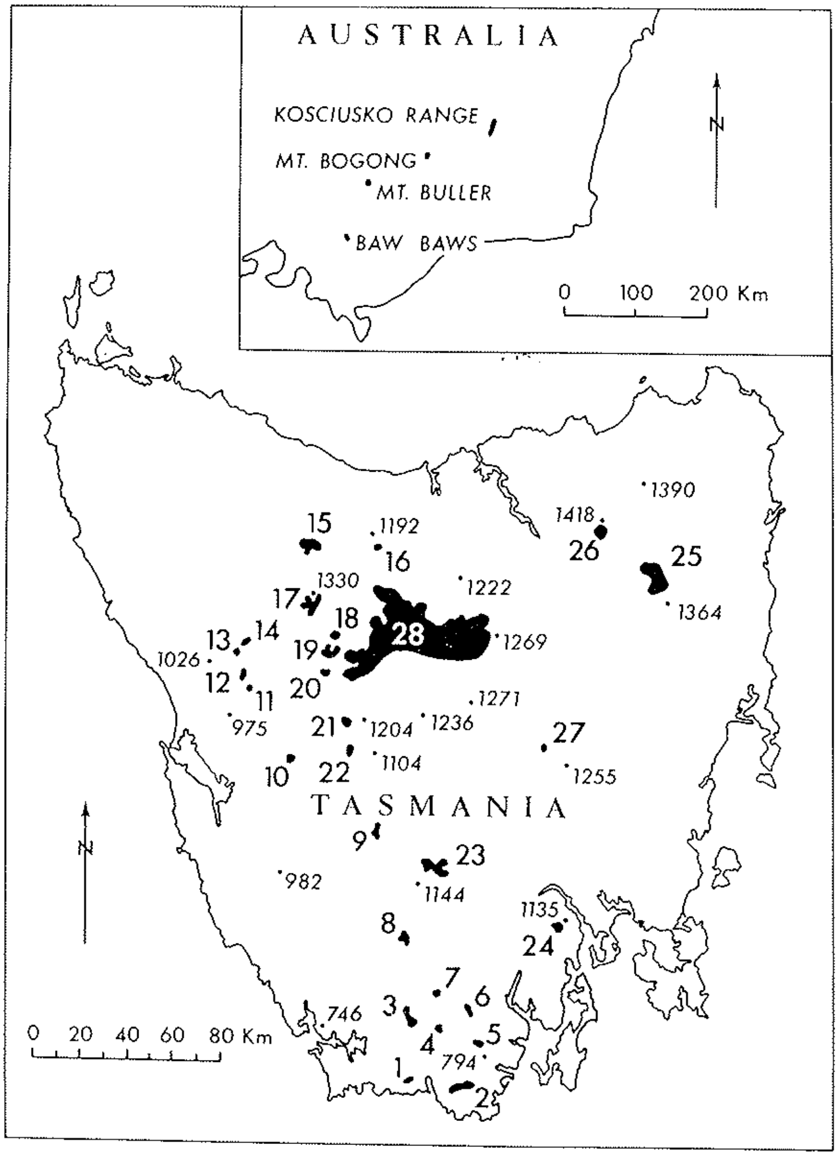

FIG. 1. The location and approximate extent of alpine vegetation covered in this study and the calculated altitudes (m) of climatic treelines (shown in italics). The mountain codes (large figures) are as follows: 1, Ironbound Range; 2, Southern Range; 3, Eastern Arthur Range; 4, Mt Bobs–The Boomerang; 5, Adamsons Peak; 6, Hartz Mountains; 7, Mt Picton; 8, Mt Anne; 9, Denison Range; 10, Frenchmans Cap; 11, Mt Sedgwick; 12, Tyndall Range; 13, Mt Read; 14, Mt Murchison; 15, Black Bluff; 16, Mt Roland; 17, Cradle Mt–Barn Bluff; 18, Mt Oakleigh; 19, Mt Ossa–Pelion East; 20, Walled Mt; 21, Mt Rufus; 22, King William Range; 23, Mt Field; 24, Mt Wellington; 25, Ben Lomond; 26, Mt Barrow; 27, Table Mt; 28, Central Plateau.

of the mainland as most of the mountain plateaux lie below 1500 m compared with the 1900 m level found in New South Wales. However, Costin (1972) places the treeline at 1200 m on Mt Wellington (24) in Tasmania as compared with 1800 m at Kosciusko in New South Wales. The single environmental correlate that best defines treeline on a global basis is a mean temperature of 10°C for the warmest month (Daubenmire, 1954). Temperature data are almost totally lacking for high altitude treeless areas in Tasmania, but the climatic treeline has been approximated by applying the environmental lapse rate of 1.3°C per 100 m to temperature data for stations on or close to mountains with treeless vegetation. The results of this analysis indicate the expected importance of continentality and latitude, with the predicted climatic treeline varying from 750 m in the coastal southwest of the state to 1400 m in the central northeast of the state (Fig. 1). The predicted climatic treelines correspond well with my observations of the upper limits of the tree form.

If alpine vegetation is defined as that above the climatic treeline the suggestion of McVean is substantially correct, there probably being nowhere in the state more than 200 m above this line, and the Central Plateau (28) and Ben Lomond (25) being the only parts of the state containing reasonably large areas of plateau country of a true alpine nature. However, exposure, cold air drainage and waterlogged soils combine to extend the range of characteristically alpine vegetation well below the climatic treeline.

The relatively sharp treelines typical of New Zealand (Wardle, 1971) and the Australian mainland (Costin *et al.*, 1979) are largely absent in Tasmania. Many of the eastern mountains have cliffs and scree slopes in the altitudinal zone in which the treeline could be expected, and where cliffs and scree slopes are absent, as on parts of Mt Wellington (24) and the King William Range (22), the dominant of the subalpine forest (*Eucalyptus coccifera*) gradually reduces in height with increased altitude and exposure, ultimately becoming a component of alpine heath. On the western mountains, wherever vascular vegetation is not excluded by lack of soil, the transition from rainforest (closed-forest) to alpine heath is equally as gradual, with many of the dominants of the alpine heath also being dominant in the subalpine rainforest (Kirkpatrick, 1977, 1980; Kirkpatrick & Harwood, 1980). On some mountains, such as the Denison Range (9) and the Ironbound Range (1), there is a narrow transition zone from the lowland *Gymnoschoenus sphaerocephalus* sedgeland to alpine vegetation dominated by the austral-montane flora, trees being largely lacking even on steep slopes because of a history of frequent firing. However, narrow transition zones between tree-dominated vegetation and alpine plant communities do occur below the climatic treeline where there is an abrupt change in drainage conditions or exposure, and where cold air drainage appears to be important in excluding trees. Fire boundaries can often give a misleading impression of an abrupt upper slope treeline, but it is only where relatively deep soils lacking rocks are found at the climatic limit of trees and the slopes allow good drainage of both water and cold air that sharp upper slope treelines can be found. Such situations are rare in Tasmania, the only known examples being on Mount Pelion East (19) and Mount Rufus (21).

The situation in Tasmania whereby vegetation largely composed of and dominated by the austral-montane element of the flora is found in both the alpine and subalpine zones makes their differentiation difficult, especially in light of the often obscure nature of the treeline. Thus, for the purpose of this study, the alpine and treeless subalpine floras are grouped for each mountain, the boundary between subalpine treeless vegetation and lowland treeless vegetation being distinct in the field on the basis of both species dominance and floristic composition.

Methods

All observed alpine vascular plant species were noted and/or collected during the course of numerous field trips in the period 1973–81. These records were supplemented from the literature for Mt Wellington (24) (Ratkowsky & Ratkowsky, 1976) and Cradle Mountain (17) (Sutton, 1928), from the unpublished work and notes of John Davies for Mt Field (23), Mt Rufus (21) and Mt Anne (8) and for all mountains from the specimens held in the herbarium of the Tasmanian Museum and Art Gallery (HO) in 1981. Species lists for Australian mainland mountains were gained from Costin *et al.* (1979), Beauglehole (1981), Willis (undated) and Scott (1974). The occurrence of Tasmanian plants in New

Zealand was gauged from Curtis (1963, 1967), Curtis & Morris (1975), Allan (1961) and Moore & Edgar (1970).

The species lists vary in completeness because of (a) the unequal amounts of time spent exploring mountains per unit area as a result of marked differences in accessibility, some requiring up to 4 days walk for access and others having roads extending into the alpine vegetation; (b) the different times of the year in which data were collected; this meant that taxa easily identifiable to species level at one time of the year were only identifiable to generic level at other times of the year, and that geophytes and annuals might have been missed on several mountains where collecting took place early in the warm season; (c) changes in taxonomic perception.

The above problems necessitated the grouping of a certain number of species for analysis and the exclusion of others. The grouped species were: *Oreobolus acutifolius* and *O. oxycarpus*; *Scirpus* spp.; *Centrolepis* spp.; *Gaimardia* spp.; *Juncus* spp.; *Luzula* spp.; *Milligania* spp.; *Danthonia* spp.; *Oreomyrrhis ciliata* and *O. eriopoda*; *Brachycome* spp.; *Cotula* spp.; *Craspedia* spp.; *Gnaphalium* spp.; *Epilobium* spp.; perennial *Euphrasia* spp.; *Ranunculus* spp.; *Viola hederacea* and *V. cunninghamii*. Orchidaceae spp. and some aquatics (*Isoetes gunnii* and *Hydatella filamentosa*) were excluded. Taxonomic nomenclature follows Curtis (1963, 1967) and Curtis & Morris (1975) for Tasmanian gymnosperms and dicotyledons, Costin *et al.* (1979) for other dicotyledons and Willis (1970) for ferns and monocotyledons except where authorities are given in Table 1.

Percentage similarity values were calculated for each pair of floras such that similarity equalled the number of species in common between the two floras divided by the number of species in the smaller flora and multiplied by 100. This measure minimizes errors

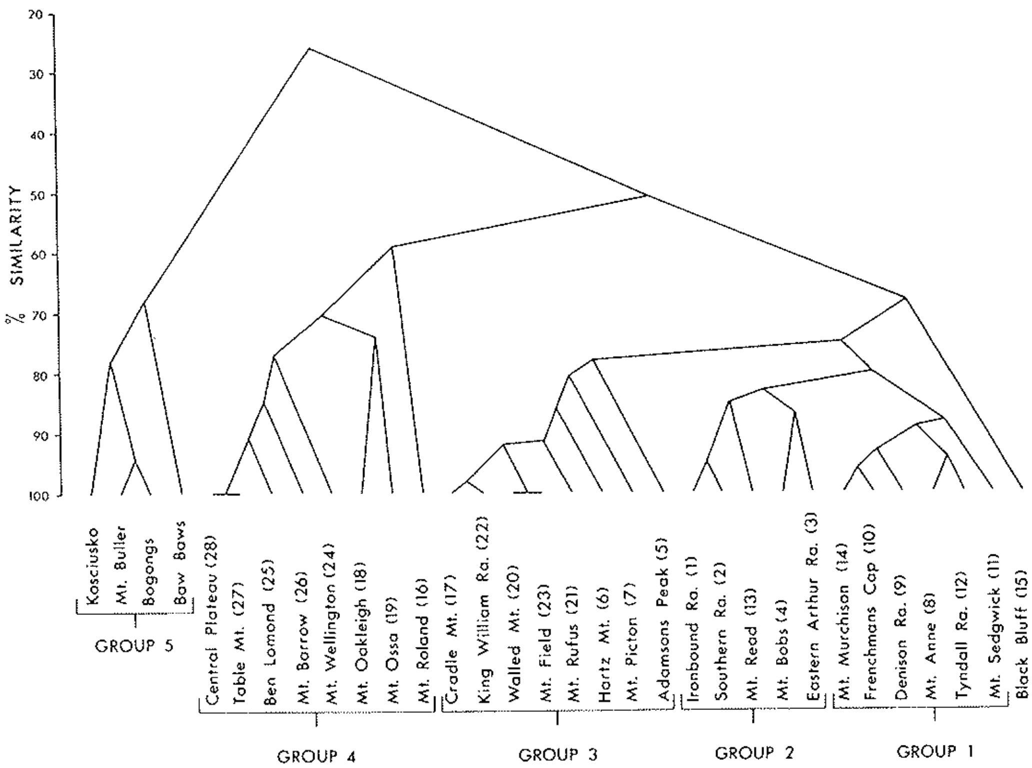

FIG. 2. Dendrogram for the polythetic agglomerative classification of the alpine floras. The groups shown are before the correction of the classification.

involved with different concentrations of data collection and different sizes of the mountain floras. Thus, a mountain with a restricted flora that is a subset of the flora of a larger mountain will have a high similarity value with that larger mountain, instead of a low value resulting from a low number of species that could possibly be in common.

The similarity matrix was used to construct a polythetic agglomerative classification of the Tasmanian and Australian mountain floras. The similarity of a fused individual with any other individual was taken to be the mean of similarity values of the floras comprising the fused individual with the other individual. The allocation of individual mountain floras to groups at the five group level was changed if the mean of the similarity values of a flora to the individuals of another group was higher than its mean similarity to the other members of its own group.

The Tasmanian mountain floras were ordinated, the distance between the poles in the ordination being the mean of the distances between each of the individuals in one floristically extreme classificatory group and each of the individuals in the other extreme group, where distance equalled 100 minus the similarity value. The distance of an individual from a pole was taken to be the mean of the distance values between that individual and the individuals in the polar group, including, where relevant, itself. The ordination score for each flora was calculated from these distance values using the method of Bray & Curtis (1956).

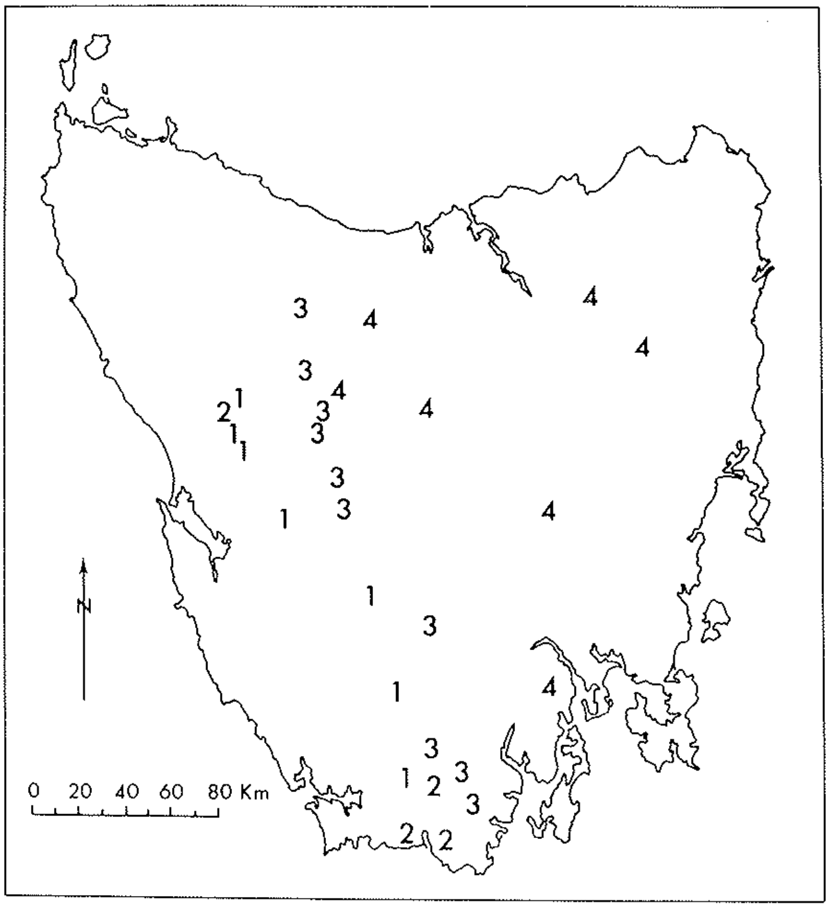

FIG. 3. The distributions of the four corrected groups in Tasmania.

Results and Discussion

At the three group level the classificatory analysis clearly differentiated the Australian mainland mountains, the eastern Tasmanian mountains and the western Tasmanian mountains (Fig. 2). Three distinct groups were perceptible in the western Tasmanian mountains. The largest of these three groups extends north–south through the centre of the state (Fig. 3), and the remaining two groups divide the mountains of the far west and southwest into those composed largely of highly quartzitic rocks and those composed of more weatherable parent material.

The two isolated northern Tasmanian mountains, Black Bluff (15) and Mt Roland (16), did not fit clearly within any of the five groups, but Black Bluff is floristically most similar to the central group (3) and Mt Roland has its greatest affinity with the eastern Tasmanian group (4). The classificatory analysis placed Mt Ossa-Pelion East (19) in group 4 and the Eastern Arthur Range (3) in group 2. These two mountains are, however, best placed in groups 3 and 1 respectively (Fig. 3).

Only group 5, consisting of the mainland mountains, could be characterized by totally faithful and constant species. These are the herbs, *Carex jackiana* and *Goodenia hederacea* and the shrubs *Tasmannia xerophila, Pimelea axiflora, P. alpina, Baeckea utilis, Richea continentis, Epacris paludosa* and *Orites lancifolia*.

Group 4 is dominated by the Central Plateau (28), the floras of Mt Barrow (26), Ben Lomond (25), Table Mt (27), Mt Oakleigh (18), Mt Wellington (24) and Mt Roland (16) being often dissimilar subsets of its flora. The shrubs *Tetratheca procumbens, Cryptandra alpina* and *Phebalium montanum* are faithful to this group and occur in more than half the floras (Table 1).

Groups 3, 4 and 5 have no totally faithful species, but each has many that are totally constant, and each can be characterized by species that attain their maximum percentage frequency in a group and are relatively less frequent outside it (Table 1).

Distance values of up to seventy-nine separate extreme pairs of the Tasmanian mountains, with most of the differences in the floras resulting from serial replacement of species of the same lifeform. For example, the green bolster plants run roughly in an east–west series *Abrotanella forsterioides, Dracophyllum minimum, Phyllachne colensoi, Donatia novae-zelandiae* and *Orites milliganii* largely displaces *O. acicularis* and *O. revoluta* on the western mountains (Fig. 4). However, the lifeform composition of the four groups does differ, with group 4 being the most distinct (Table 2). The percentage of fern and graminoid species is relatively uniform between the four groups, although the number of Poaceae species is greatest on the eastern mountains. The percentages of mat and rosette herbs and cushions and mat shrubs are greater for groups 3 and 4 than for 1 and 2. Groups 3 and 4 have lower percentages of nanophanerophytes than 1 and 2, and group 4 has a greater proportion of annuals and geophytes and a lesser proportion of plants of cushion form than the other three groups.

The west to east floristic gradient is well illustrated by the contour map of ordination scores and the linkage map (Figs. 5 and 6). This gradient does not correlate well with continentality (r = 0.4427), but is strongly related to both mean annual precipitation and surface geology. The most recent precipitation map for the state (Australian Bureau of Meteorology, unpublished) was used to extract mean annual precipitation figures for each mountain to the nearest 100 mm. There is a strong linear relationship between these figures and the ordination scores (Fig. 7, r = –0.6637), except that the southwestern mountains appear to have lower precipitation figures than could be expected from their ordination scores (Fig. 7). Given the otherwise strong linear relationship between precipitation and ordination scores (r = –0.9294 with mountains 1–9 excluded), the strong relationship that also exists in this group and the remarkably few stations from which the part of the map containing the southwest was constructed (none of which were on any of the mountains), it seems reasonable to suggest that the map severely underestimates precipitation on the mountains in this sector of the state. Cloud cover, surface geology, the height of the climatic treeline and seasonal distribution of precipitation are all similar between at least some of the mountains in the southwest and those with similar ordination

TABLE 1. The percentage frequency by classificatory group of all species occurring on half or more of the mountains in at least one Tasmanian group

Species	Group				
	5	4	3	2	1
Ferns					
Lycopodium fastigiatum	100	71	100	100	100
Polystichum proliferum	100	86	70	25	43
Huperzia selago (L.) Bernh. ex Schrank & Mart.	75	29	50	25	57
Gleichenia alpina R.Br.	0	71	70	75	43
Lycopodium scariosum	50	57	90	75	43
Gleichenia abscida Rodway	0	0	0	50	29
Blechnum wattsii Tindale	0	0	20	100	100
Monocotyledons					
Empodisma minus	100	100	100	100	100
Astelia alpina	100	87	100	100	100
Luzula spp.	100	100	100	75	100
Juncus spp.	100	57	50	25	14
Oreobolus distichus	100	71	40	0	14
Agrostis spp.	100	71	60	0	29
Hierochloe redolens	75	57	50	0	0
Scirpus spp.	75	57	50	50	43
Carex gaudichaudiana	75	57	70	25	14
Deyeuxia monticola	75	100	70	50	57
Restio australis	25	86	40	0	14
Poa gunnii Vickery	0	100	100	100	57
Centrolepis spp.	0	43	70	50	57
Carpha alpina	25	86	100	100	100
Oreobolus acutifolius Blake[1]	0	43	100	100	100
O. pumilio	75	71	100	100	100
Uncinia compacta	75	57	80	100	100
Blandfordia punicea Sweet	0	14	40	100	100
Microlaena tasmanica Hook	0	14	50	100	100
Danthonia spp.	75	71	80	100	43
Hierochloe fraseri Hook	0	71	80	100	71
Milligania spp.	0	14	90	100	57
Schoenus calyptratus	75	57	60	100	0
Gahnia grandis	0	0	50	100	71
Campynema lineare Labill.	0	14	60	75	43
Diplarrhena latifolia Benth.	0	29	70	75	71
Isophysis tasmanica (Hook.) T. Moore	0	0	29	75	86
Restio complanatus	0	29	40	50	57
Xyris marginata Rendle	0	0	20	50	57
Dicotyledonous Herbs					
Euphrasia spp.	100	100	100	100	100
Gentianella diemensis	100	71	100	100	100
Senecio pectinatus	100	71	100	100	100
Celmisia longifolia sensu lato	100	86	100	75	100
Oreomyrrhis ciliata[2]	100	43	40	50	43
Erigeron pappachroma	100	57	50	0	86
Epilobium spp.	100	71	80	0	14
Geranium potentilloides	100	71	30	0	29
Gnaphalium spp.	100	86	60	50	14
Acaena novae-zelandiae	100	86	50	0	14
Stylidium graminifolium	100	43	50	50	29
Craspedia spp.	100	57	30	0	29
Brachycome spp.	100	71	30	0	0
Helichrysum scorpioides	75	71	40	0	14

Table 1 – *continued*

Species	Group				
	5	4	3	2	1
Viola hederacea[3]	75	71	60	0	0
Gonocarpus montanus	50	100	70	75	29
Plantago tasmanica	50	100	90	75	0
Hydrocotyle sibthorpioides	50	86	50	0	14
Senecio gunnii	50	71	10	0	0
Oreomyrrhis sessiliflora	0	57	40	25	0
Wahlenbergia saxicola	0	57	30	0	14
Hypericum japonicum	25	57	10	0	0
Velleia montana	0	57	10	0	0
Poranthera microphylla	50	57	10	25	0
Erigeron stellatus	0	29	100	100	100
Drosera arcturi	75	57	100	100	100
Ewartia meredítheae	0	0	100	75	86
E. planchonii	0	14	100	75	29
Rubus gunnianus	0	71	90	75	71
Scaevola hookeri	50	57	70	0	14
Plantago daltonii	0	43	60	50	14
Actinotus moorei	0	0	60	100	100
A. suffocata	0	0	70	100	86
Abrotanella scapigera	0	0	80	100	57
Senecio leptocarpus	0	57	90	100	86
Mitrasacme montana	50	57	80	100	43
Oxalis lactea	25	29	90	100	57
Acaena montana	0	43	80	100	29
Euphrasia hookeri	0	0	30	100	86
Dichosciadeum ranunculaceum	25	0	70	75	57
Forstera bellidifolia	0	0	50	75	71
Geum talbotianum	0	0	30	50	29
Senecio primulifolius	0	0	0	50	14
S. papillosus	0	0	10	50	0
Helichrysum pumilum	0	0	30	75	100
Anemone crassifolia	0	0	30	75	100
Helichrysum milliganii	0	14	60	75	86
Celmisia saxifraga	0	29	80	75	86
Diplaspis cordifolia	0	0	40	75	86
Shrubs					
Podocarpus lawrencii	100	57	100	50	71
Baeckea gunniana	100	100	70	0	43
Olearia phlogopappa	100	71	30	0	29
Helichrysum hookeri	100	57	30	0	0
Grevillea australis	100	57	0	0	0
Coprosma pumila	75	57	50	0	0
Coprosma nitida	75	100	100	100	100
Pentachondra pumila	75	100	100	100	100
Drimys lanceolata	25	100	100	100	100
Exocarpos humifusus	0	100	90	100	100
Richea sprengelioides	0	100	100	100	86
Cyathodes parvifolia	0	100	80	100	86
Oxylobium ellipticum	75	86	50	0	43
Pimelea sericea	0	86	50	75	14
Lissanthe montana	50	71	50	0	14
Monotoca empetrifolia	0	71	20	0	0
Pultenaea subumbellata	0	71	20	0	0
Tetratheca procumbens	0	71	0	0	0
Phebalium montanum	0	57	0	0	0
Cryptandra alpina	0	57	0	0	0

Table 1 – *continued*

Species	Group				
	5	4	3	2	1
Epacris gunnii	0	57	10	0	0
Richea acerosa	0	57	40	0	0
Pernettya tasmanica	0	57	40	0	0
Trochocarpa thymifolia	0	57	30	50	0
Helichrysum backhousii	0	71	100	75	100
Olearia ledifolia	0	71	100	100	86
Orites revoluta	0	86	100	100	71
Cyathodes dealbata	0	71	100	75	100
Epacris serpyllifolia	0	86	100	100	100
Richea scoparia	0	86	100	100	100
Orites acicularis	0	71	100	75	29
Leptospermum rupestre	0	71	100	0	14
Mitrasacme archeri	0	14	100	75	86
Microcachrys tetragona	0	29	90	75	86
Eucalyptus coccifera	0	71	90	0	14
Ourisia integrifolia	0	57	90	50	14
Cyathodes straminea	0	71	90	0	29
Dracophyllum minimum	0	0	80	75	71
Coprosma moorei	25	43	60	25	29
Gaultheria depressa	0	14	50	0	29
Olearia tasmanica	0	43	50	100	100
Bauera rubioides	0	57	80	100	100
Archeria serpyllifolia	0	0	90	100	100
Sprengelia incarnata	0	29	80	100	100
Agastachys odorata	0	0	40	100	100
Persoonia gunnii	0	0	80	100	100
Donatia novae-zelandiae	0	0	80	100	100
Nothofagus cunninghamii	25	86	80	100	100
Cenarrhenes nitida	0	0	60	100	100
Eucalyptus vernicosa	0	0	40	100	100
Athrotaxis selaginoides	0	14	40	100	100
Olearia pinifolia	0	71	70	100	86
Bellendena montana	0	71	80	100	29
Tetracarpaea tasmanica	0	0	60	100	86
Trochocarpa cunninghamii	0	0	40	100	57
Richea pandanifolia	0	0	80	100	86
Abrotanella forsterioides	0	71	30	75	29
Dracophyllum milliganii	0	0	20	75	71
Monotoca aff. *linifolia*	0	29	20	75	29
Trochocarpa gunnii	0	0	20	75	71
Orites diversifolia	0	14	60	75	43
Pterygopappus lawrencii	0	43	70	75	71
Archeria hirtella	0	0	20	75	29
Archeria comberi	0	0	30	0	100
Cyathodes petiolaris	0	43	80	25	100
Richea milliganii	0	0	20	25	100
Eucryphia milliganii	0	0	40	75	100
Orites milliganii	0	0	0	50	100
Leptospermum nitidum	0	0	60	75	100
Nothofagus gunnii	0	29	60	75	100
Diselma archeri	0	29	70	75	100
Athrotaxis cupressoides	0	29	60	50	86
Monotoca submutica	0	0	60	75	86
Leucopogon milliganii	0	0	20	25	86
Anodopetalum biglandulosum	0	0	0	75	86
Prionotes cerinthoides	0	0	20	75	86

[1] Includes *O. oxycarpus*; [2] includes *O. eriopoda*; [3] includes *V. cunninghamii*.

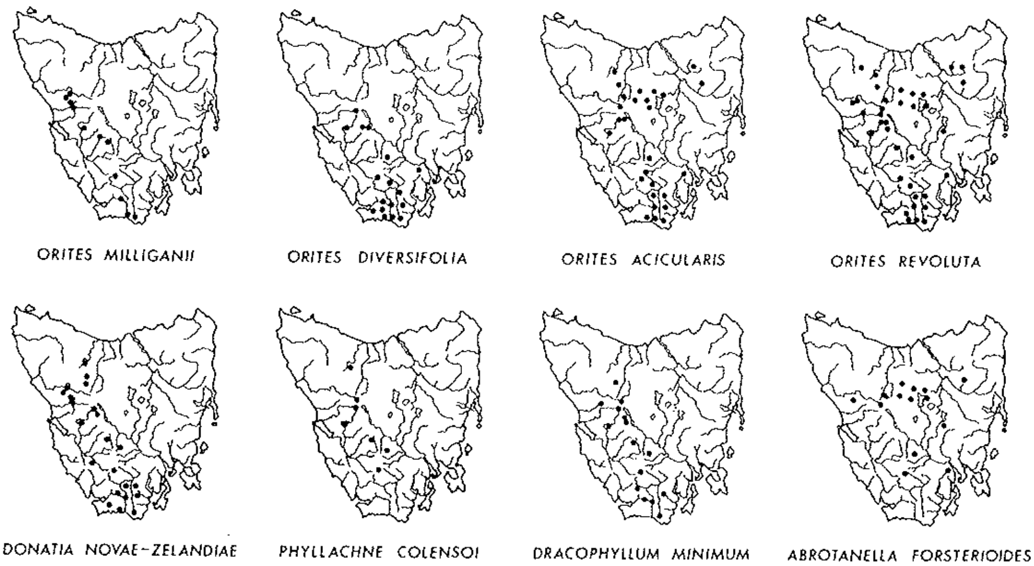

FIG. 4. The distributions of the four species of *Orites* and the green bolster plant species in the alpine vegetation of Tasmania. The records are from the fieldwork of the author and the specimens held in the herbarium of the Tasmanian Museum and Art Gallery.

scores further north, invalidating these factors as explanations for the anomaly.

The relationship of floristic variation to surface geology was expressed by giving each mountain a score of 0 for the presence of quartzitic rocks, 2 for the presence of dolerite and/or basalt and 1 for the presence of rocks of intermediate weatherability and dividing by the number of rock types present. The mountains scoring 0 have a mean ordination score of 10.25 which encompasses a range from 0.5 to 32.0; those scoring 1.0 have a mean of 14.5 with a range from 8.5 to 24.0; those scoring 1.5 have a mean of 17.0 with a range from 8.5 to 32.0; and those scoring 2.0 have a mean of 34.1 with a range from 19.5 to 47.0. The role of substrate in floristic differentiation may be subordinate to that of moisture availability in the same way as is suggested for local gradients by Billings & Mooney (1968). However, there is no doubt that the vegetation on different substrata is floristically distinct in the contiguous situation as in the case of Mt Bobs and the Boomerang (4) (Kirkpatrick & Harwood, 1980) where dolerite, sandstone and mudstone are adjacent, and as at Cradle Mountain where quartzite and dolerite are adjacent. Nevertheless the dolerite flora on Mt Bobs (17) has more in common with the quartzite flora of the Eastern Arthur Range (3) than it does with the dolerite floras of the eastern, dry mountains, and the quartzite

TABLE 2. Lifeform analysis of the Tasmanian classificatory group floras

	Group means			
	1	2	3	4
% Ferns	5.8	5.5	5.6	5.0
% Graminoids	19.0	19.5	18.7	18.6
% Annuals and geophytes	3.1	3.2	2.9	4.9
% Mat and rosette herbs	22.3	24.7	27.9	28.0
% Cushion*	7.1	6.5	7.0	3.0
% Cushion and mat shrubs	10.4	9.7	13.2	12.0
% Nanophanerophytes	41.3	37.2	32.0	31.9

*Includes species in other lifeform groups.

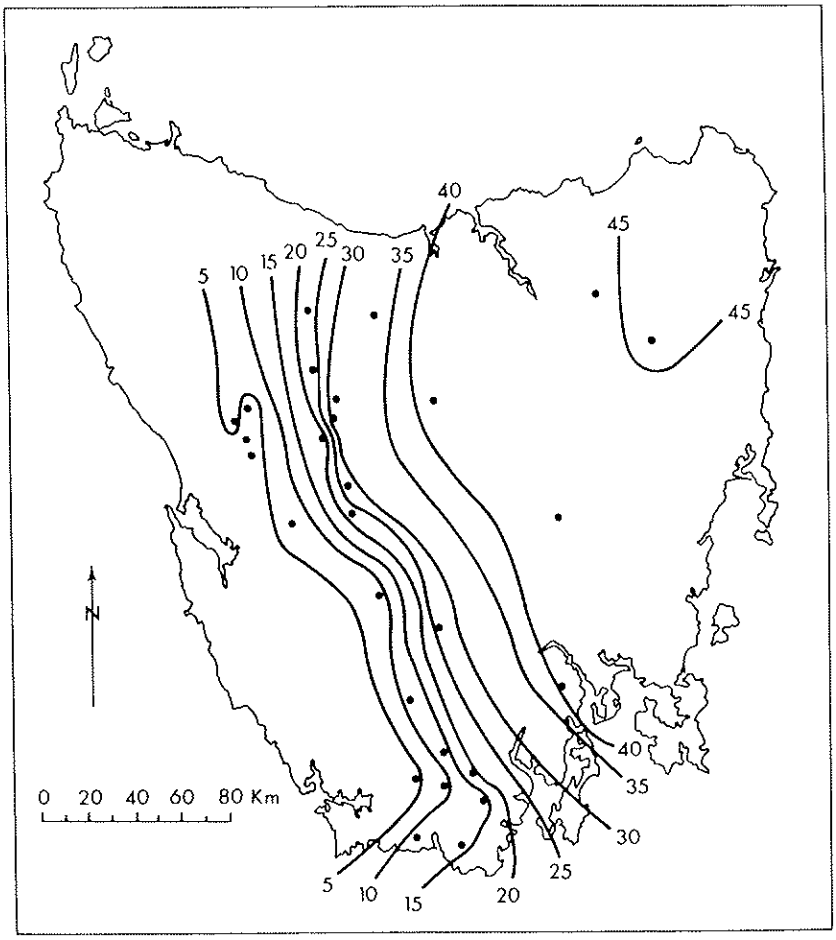

FIG. 5. Contour map of ordination scores for the Tasmanian alpine floras.

flora of Mt Roland (16) has greater affinities with the dolerite floras of other mountains with low precipitation than with the high rainfall quartzite mountain floras.

The tendency for a siliceous substratum to be associated with a shift in the affinities of a flora towards those of wetter mountains suggests that soil conditions may be critical in differentiating the floras. High rainfall and siliceous substrata both contribute towards low nutrient availability and high acidity. The development of deep soils has been inhibited on the western mountains by the truncating effects of glacial and periglacial activity and the low weatherability of the substrate, whereas the eastern mountains are not only more easily weatherable but also have considerable areas of glacial and periglacial deposits in the altitudinal range occupied by alpine vegetation. Peat deposits tend to be deeper on the eastern mountains, where they are largely confined to flats, than in the western mountains where they can be found on all but the steepest slopes. Alpine humus soils are totally lacking in the western mountains but are relatively common in the east.

It is somewhat difficult to gauge whether drought stress would be greater in the eastern than in the western mountains. I have observed death through droughting in the eastern mountains, but never in the west. However, the extreme shallowness of both mineral and organic soils in the west suggests that droughting could occur. Cases of peat destruction by fire in the western mountains testify to occasional drought.

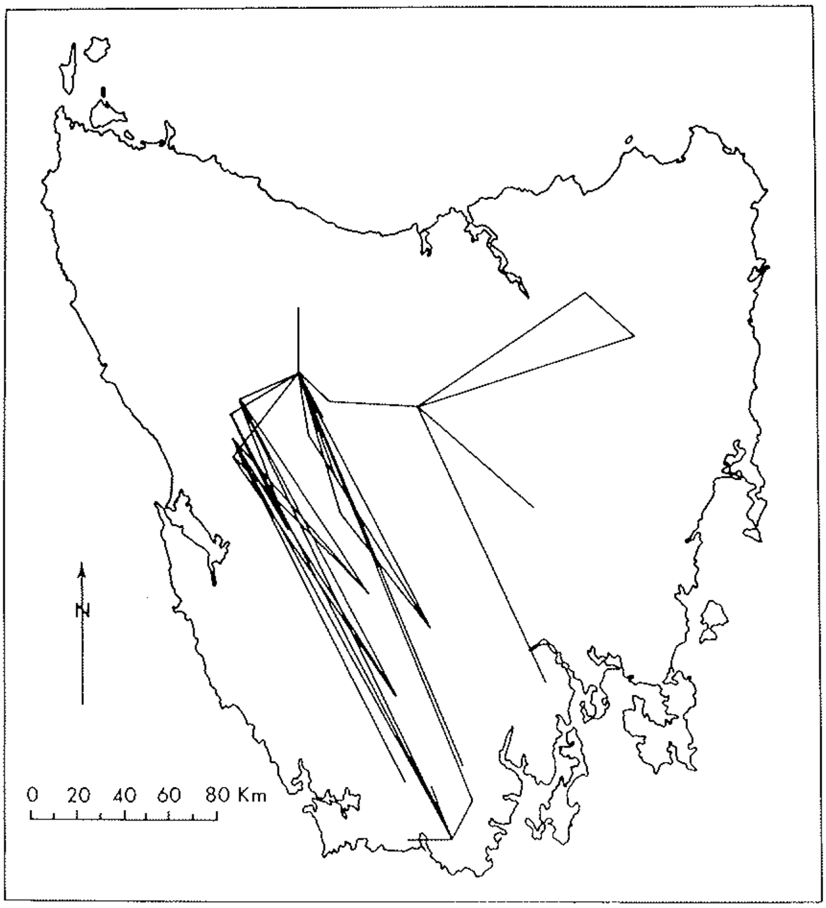

FIG. 6. Linkage map. The lines join mountains with percentage similarity values of 90 or more.

Fire frequency is another environmental variable that is related to precipitation. Macphail (1980) suggests on the basis of palaeodata that the relationship is negative in Tasmania, and the absence of almost all of the most fire susceptible species from the eastern mountains (Fig. 8) supports this contention. *Podocarpus lawrencii* is the only highly fire-susceptible species to occur in the east, undoubtedly largely due to the fire-protected nature of its block stream habitat, and perhaps partially due to its relatively wide dispersal by birds.

The western Tasmanian alpine vegetation is characterized by a high degree of Tasmanian endemism. There is a strong linear inverse relationship between the percentage of endemic taxa and the ordination score (Fig. 9, $r = -0.9161$), with endemism varying from almost 60% at the western extreme to less than 30% on some of the easternmost mountains. Mt Sedgwick (11) and Mt Roland (16) have a lesser proportion of endemics than could be expected given their ordination scores, possibly a function of the small area of their alpine vegetation and the low elevation of their peaks in relation to the climatic treeline.

The floras of the eastern mountains have the greatest affinity with those of the mainland mountains and New Zealand. There are strong positive linear relationships between the ordination scores and the similarity values between Tasmanian mountains and Kosciusko ($r = 0.9361$), the Bogong High Plains ($r = 0.9504$), Mt Buller ($r = 0.7955$), the Baw Baws ($r = 0.8669$) and New Zealand ($r = 0.8213$). Similarity values vary from 18 to

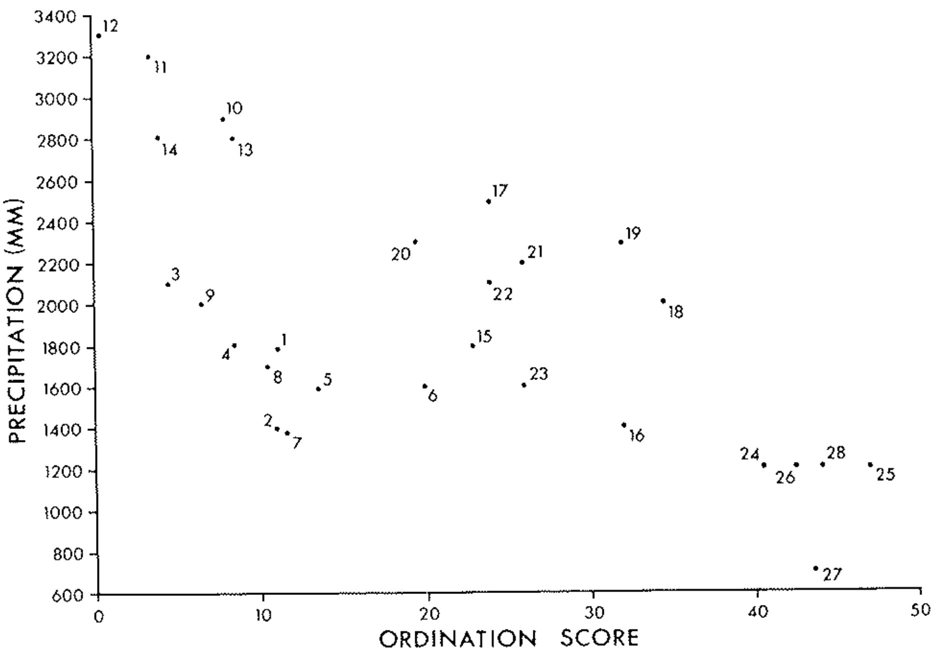

FIG. 7. The relationship between mean annual precipitation and the ordination scores.

51 with a mean of 30 for Kosciusko (Fig. 10) from 19 to 55 with a mean of 33 for the Bogong High Plains, from 10 to 59 with a mean of 28 for Mt Buller, from 21 to 58 with a mean of 35 for the Baw Baws (Fig. 10) and from 17 to 34 with a mean of 24 for New Zealand (Fig. 11). Several of the eastern Tasmanian mountain floras are more similar to those of the mainland mountains than to those in the far west of the state. For example,

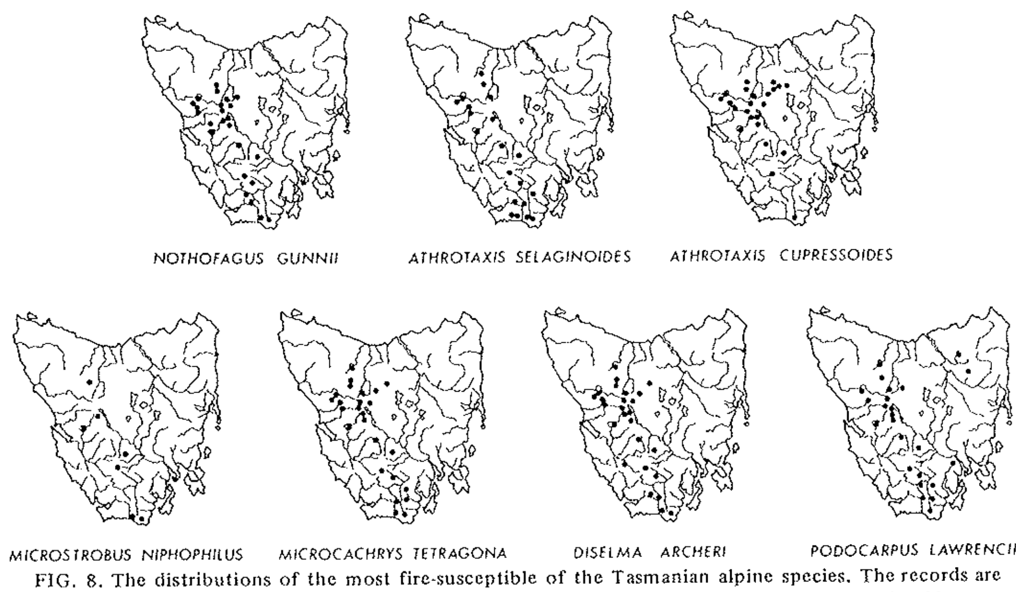

FIG. 8. The distributions of the most fire-susceptible of the Tasmanian alpine species. The records are from the fieldwork of the author and the specimens held in the herbarium of the Tasmanian Museum and Art Gallery.

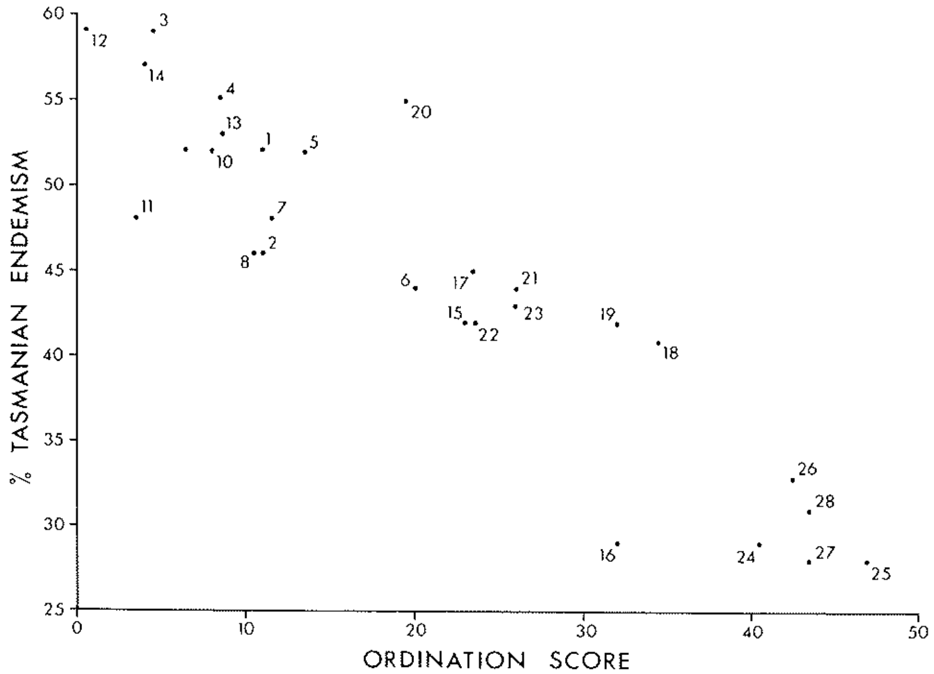

FIG. 9. The relationship between Tasmanian endemism and the ordination scores.

the Tyndall Range (12) has a similarity value of 36 with Ben Lomond (25), which in turn has similarity values of 48 with Kosciusko, 62 with the Bogong High Plains, 54 with Mt Buller and 51 with the Baw Baws. Thus, the mainland mountains could be considered one extreme of an alpine floristic continuum of which the far western Tasmanian mountains comprise the other extreme, most of this continuum being within Tasmania, the minimum similarity value between any of the mainland mountains being 63 for the comparison between Kosciusko and the Baw Baws. However, the mainland mountains do not sit easily within the precipitation sequence established for Tasmania, Kosciusko receiving approximately 2300 mm per annum, the Bogong High Plains receiving 2300 mm per annum, Mt Buller receiving 1600 mm per annum and the Baw Baws receiving 1800 mm per annum and the percentage of rain received in summer being generally lower in Tasmania.

The major environmental differences between the mainland and Tasmanian mountains are in the duration and variability of snow cover and the nature of the soils. The more continental location of the mainland mountains results in colder winters and longer and more persistent snow cover than are experienced anywhere in Tasmania. There is a worldwide association between long and persistent snow cover and grassland and herbfield alpine vegetation, and a similar association between alpine sites usually free of snow in winter and the dominance of cushion plants and prostrate shrubs (Billings & Mooney, 1968). In keeping with these associations the mainland mountains are mainly covered with grassland and herbfield, and those of Tasmania, especially in the west, have vegetation almost totally dominated by shrubs. This variation in dominance is reflected in the proportions of herbs and shrubs in the alpine floras. On the mainland mountains herbs constitute 69–76% of the floras, whereas in Tasmania the range is from 44% to 64% with a mean of 53%.

However, it seems that persistence and longevity of snow cover may be more important in its effects on soil formation than in its direct effects on the vegetation. Grassland and herbfield are largely associated with alpine humus soils, which are both relatively deep and free of rocks. Shrubs displace

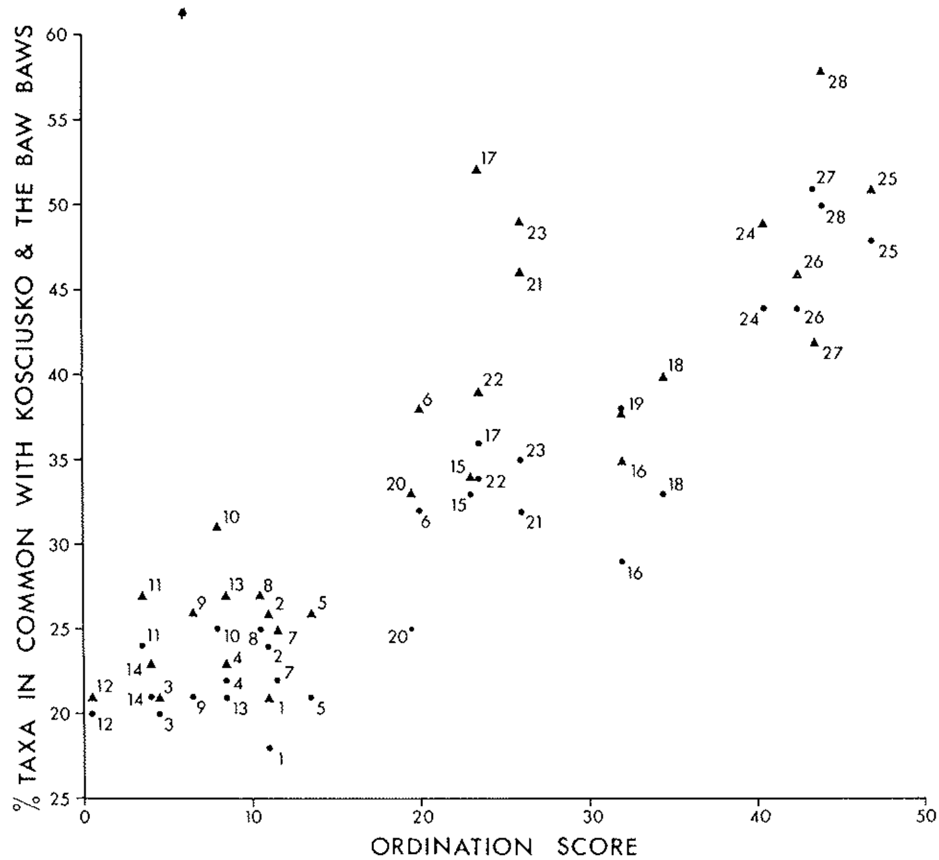

FIG. 10. The relationships between the ordination scores and the percentage similarity values with Kosciusko (dots) and the Baw Baws (triangles).

grasses on shallow rocky soils, in bog situations, and where deep soils are covered with a lag deposit of rocks. Soil mountains may exist on the mainland largely because the soil is protected from ice-heaving, needle ice formation and wind and water erosion by a persistent snow cover in the coldest part of the year, whereas there are few situations on the mountains in Tasmania where such protection prevails through the winter. The widespread Tasmanian bog peats give some protection from periglacial processes but favour shrub dominance. The less severe glaciation experienced on the mainland may also have contributed towards the contrast between soil and rock mountains. In the western Tasmanian mountains alpine vegetation is almost totally confined within the erosional limits of the Last Glaciation, whereas depositional features are contained well within the alpine areas of the mainland. The relatively moist summers experienced on the mainland mountains may have also played a role in increasing the rate of postglacial weathering relative to that which has occurred in Tasmania.

The preceding analyses and discussion have shown that the Tasmanian alpine floras are considerably more heterogeneous than those of the mainland and have suggested that much of the variation within and between the Tasmanian and mainland alpine floras may be related to edaphic factors. However, this latter suggestion must be considered only a working hypothesis given the paucity of knowledge of Tasmanian alpine soils and the edaphic responses of Tasmanian plant species and communities.

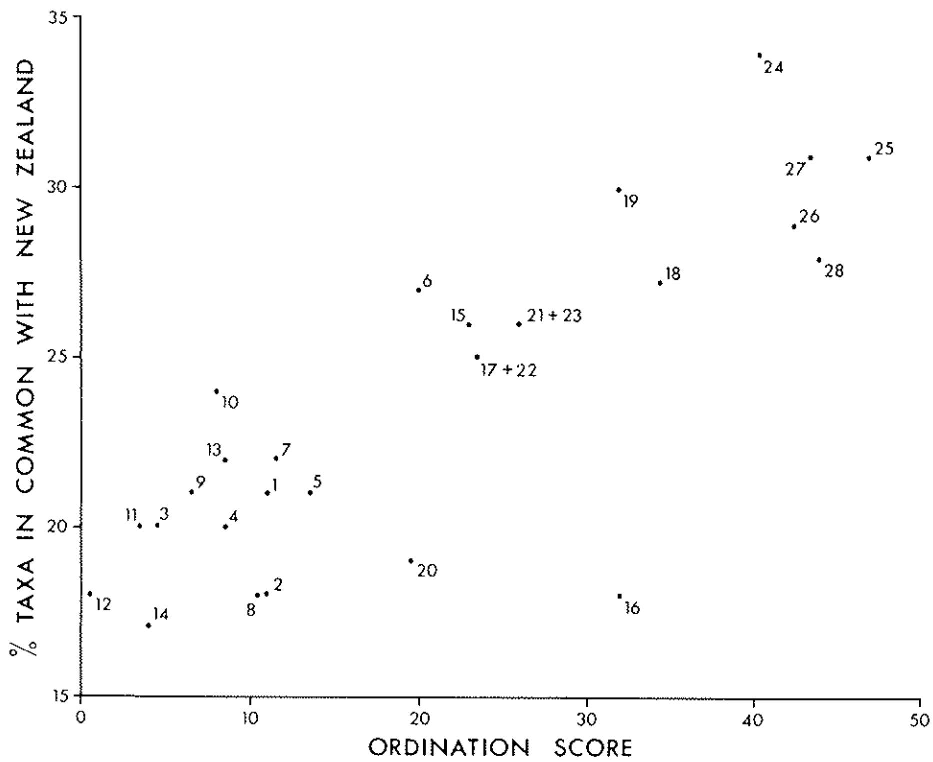

FIG. 11. The relationship between the ordination scores and the similarity values with New Zealand.

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